

Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests

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Numerical superiority confers a competitive advantage during contests among animal groups, shaping patterns of resource access, and, by extension, fitness. However, relative group size does not always determine the winner of intergroup contests. Smaller, presumably weaker social groups often defeat their larger neighbors, but how and when they are able to do so remains poorly understood. Models of competition between individuals suggest that location may influence contest outcome. However, because of the logistical difficulties of studying intergroup interactions, previous studies have been unable to determine how contest location and group size interact to shape relationships among groups. We address this question by using an automated radio telemetry system to study intergroup interactions among six capuchin monkey (*Cebus capucinus*) social groups of varying sizes. We find that the odds of winning increase with relative group size; one additional group member increases the odds of winning an interaction by 10%. However, this effect is not uniform across space; with each 100 m that a group moves away from the center of its home range, its odds of winning an interaction decrease by 31%. We demonstrate that contest outcome depends on an interaction between group size and location, such that small groups can defeat much larger groups near the center of their home range. The tendency of resident groups to win contests may help explain how small groups persist in areas with intense intergroup competition.

between-group competition | intergroup dominance | payoff asymmetries | resource holding potential

In social species ranging from ants to humans (1, 2), groups compete over access to resources, such as food (3–5), mates (6), and water (7), that are critical for survival and reproduction. Competitive ability increases with group size in many species (1, 2, 8–13), and this trend is thought to provide a selective pressure favoring group living (14–17). Numerical superiority, however, does not ensure victory (3, 18–21). Even in species where group size strongly predicts the outcome of intergroup contests, small groups are frequently victorious (3). When and how groups are able to overcome a numerical disadvantage are critical factors determining the costs and benefits of grouping, but remain poorly understood.

Theoretical work on contests between individuals provides a useful framework for thinking about contests among groups. Models of competition between individuals suggest that contest outcome depends on two fundamental factors (22). First, asymmetries in fighting ability [resource holding potential (RHP)] may reliably predict which individual prevails (23). Second, asymmetries in payoff (the consequences of winning or losing an interaction) may affect the intensity with which contestants compete. Location-based payoff asymmetries arise if residents place a higher value on the area being contested than intruders, and thus have more to gain from winning the interaction (or more to lose in defeat) (22, 24). Home range centers, for example, might be more valuable than peripheral areas if ranges

are established in areas of particularly high resource density, if knowledge gained through frequent use of an area creates foraging advantages (25), or if competition with neighbors decreases foraging efficiency in peripheral areas (26, 27). For similar reasons, frequently used areas might be highly valued regardless of their position in the home range.

Intergroup competition is more complex than interindividual competition because it depends on the actions of multiple independent participants. For example, group size likely determines the maximum RHP of a group, but the number of individuals who decide to participate in any given interaction determines the realized RHP. Nonetheless, it is likely that the same factors that are important in contests between individuals also influence the outcome of contests among groups.

Despite its role in shaping access to resources, few studies have investigated which factors predict success in intergroup competition (but see refs. 28–30), and none has investigated how group size and contest location interact to determine the outcome of competitive interactions. This topic has been neglected in part because intergroup contests are relatively infrequent, making it difficult to obtain a sufficient sample size to distinguish between competing hypotheses. The logistical difficulties of simultaneously following multiple social groups also make such studies expensive and time consuming. Finally, differences in habituation level across study groups are a concern when traditional observation techniques are used to investigate intergroup competition because the presence of an observer may influence contest outcome. The behavioral reaction of less habituated groups to the observer may negatively impact their chances of winning an interaction and artificially inflate the competitive success of well habituated groups.

We overcame these challenges by using an Automated Radio Telemetry System (ARTS) to simultaneously monitor the movements of six white-faced capuchin (*Cebus capucinus*; hereafter capuchin) social groups on Barro Colorado Island, Panama, from November 2004 to April 2005. ARTS enabled us to detect many more intergroup interactions than traditional techniques would have yielded in an equivalent period (see Table 1). It also provided a quantitative and unbiased method for identifying and determining the outcome of interactions by using spatial criteria. By using ARTS, we are able to address a long-standing question regarding intergroup relationships that had proved intractable with traditional data-collection methods.

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Table 1. Summary of data collection for the six social groups

Group	No. of adults	Animal ID	Sex	No. of locations	Data-collection period
TB	6	51	F	10,638	11/04–04/05
		87	F	4,147	03/05–04/05
BLT	5	52	M	8,515	11/04–04/05
		53	F	9,665	11/04–04/05
Top	10	54	F	8,000	11/04–04/05
		55	M	10,653	11/04–04/05
BL12	13	57	F	7,871	11/04–04/05
		58	M	7,437	11/04–04/05
FC	10	83	F	1,667	03/05–04/05
		84	F	1,662	03/05–04/05
Conrad	10	85	F	2,242	03/05–04/05
		86	F	2,073	03/05–04/05

Animal ID is the individual identifier of radio-collared animals, no. of locations is number of location estimates recorded by ARTS, and data-collection period refers to the time period when ARTS data were collected for each individual.

Intergroup competition in capuchins is intense and occasionally lethal (31). Although group size is highly variable (32), previous research has shown that large groups do not necessarily defeat small groups (19). However, the effect of contest location on the outcome of intergroup encounters has not been assessed, and the relationship between group size and contest location has never been explored. Here we investigate the effects of group size, which is thought to determine a group's maximum RHP (33–35), and measures of location, which may create payoff asymmetries (36, 37), on the outcome of competitive intergroup encounters among capuchin social groups. Because males play a more prominent role in intergroup contests than females in this species (19, 38), and may therefore contribute more to the RHP of a group, we also investigate the importance of the relative number of adults of each sex in the group.

Results

We identified 58 intergroup interactions in which one social group spatially displaced another (Fig. 1; see *Materials and Methods* for criteria used to define a displacement). Clear dominance relationships were only observed in two of eight group dyads. Relations between some groups were strongly one sided (BLT defeated TB in 12 of 15 interactions), but others were more evenly matched (BLT defeated FC in 5 of 13 interactions).

Large relative group size (focal group size minus opposing group size) conferred a competitive advantage. The odds of

Table 2. Output from a GEE multiple regression of focal group–intergroup interaction success probability versus relative group size (focal group size minus opposing group size) and location (distance from focal group's home range center in meters)

Variable	Parameter estimate	Standard error	χ^2_1	<i>P</i>
Intercept	1.56	0.63	6.2	0.01
Relative group size	−0.07	0.07	1.2	0.28
Location	−0.39	0.18	4.6	0.03
Group size by location	0.05	0.02	4.0	0.05

winning increased by 10% with each one-individual increase in relative group size [Generalized Estimating Equations (GEE) logistic regression, odds ratio: 1.10, $\chi^2_1 = 11.8$, $P = 0.0006$, repeated measure = dyad]. Given that male capuchins are typically more consistent and aggressive participants in intergroup conflicts (19, 38), we explored the effect of the relative number of members of each sex on the likelihood of winning an interaction. Groups with relatively more males were more likely to win (GEE logistic regression, odds ratio: 1.68, $\chi^2_1 = 24.6$, $P < 0.0001$, repeated measure = dyad), as were those with relatively more females (GEE logistic regression, odds ratio: 1.13, $\chi^2_1 = 7.6$, $P = 0.006$, repeated measure = dyad). Because the number of males and females in a group were highly correlated ($R^2 = 0.95$, $P < 0.001$), we were unable to use multiple regression to determine whether the relative group size effect was driven by one sex or the other.

Although relatively larger groups were significantly more likely to win interactions, they did not always do so. For example, BLT won almost half of its interactions with Top, which had twice as many adults (Fig. 1). Additionally, the tendency to win was not transitive; although BL12 consistently beat BLT and BLT and Top were evenly matched, BL12 did not consistently beat Top. These results indicate that factors other than relative group size also influenced interaction outcome.

Indeed, as predicted, interaction location played an important role in determining the victor. Groups were more likely to win interactions close to the center of their home range. For every 100-m increase in distance from the center of its home range, a group's odds of winning decreased by 31% (GEE logistic regression, odds ratio: 0.69, $\chi^2_1 = 8.5$, $P = 0.0036$, repeated measure = dyad). For example, on both occasions when BLT (5 adults) defeated BL12 (13 adults), the interaction took place relatively close to the center of BLT's home range (175 and 325 m, respectively). However, the degree to which the focal group had used the contested area in the 2 weeks before the interaction did not affect the interaction outcome (GEE logistic regression, $\chi^2_1 = 0.34$, $P = 0.56$, repeated measure = dyad) even when controlling for relative group size ($\chi^2_1 = 0.53$, $P = 0.51$). These results suggest that geometric location within the home range, but not the intensity of use, tempers the effect of group size.

To more fully test this idea, we used a saturated GEE multiple logistic regression model (repeated measure = dyad) to examine the relationship among relative group size, location, and the probability of winning an interaction. Location (distance from the focal group's home range center) and the two-way interaction term (location by relative group size) were both statistically significant predictors of victory (Table 2). To aid in interpreting these results, we used the model parameters to predict the probability of winning for all combinations of relative group size and location (Fig. 2). All groups, regardless of size, were highly likely to win interactions that occurred close to the center of their home range. With increasing distance from the center of a group's home range, the probability of winning an intergroup

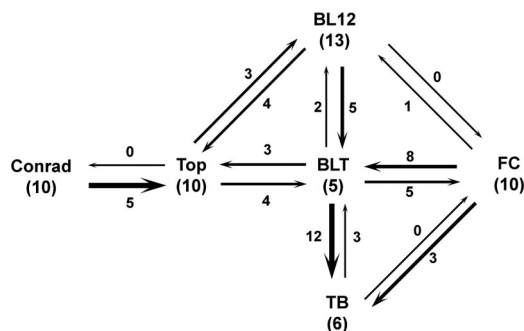


Fig. 1. Summary of 58 intergroup interactions among the six social groups. Numbers in parentheses indicate the number of adult monkeys per group. Arrows point from winner to loser. Relative arrow thickness and associated numbers indicate sample sizes. For example, BL12 (13 individuals) defeated BLT (5 individuals) five times, and BLT defeated BL12 twice.

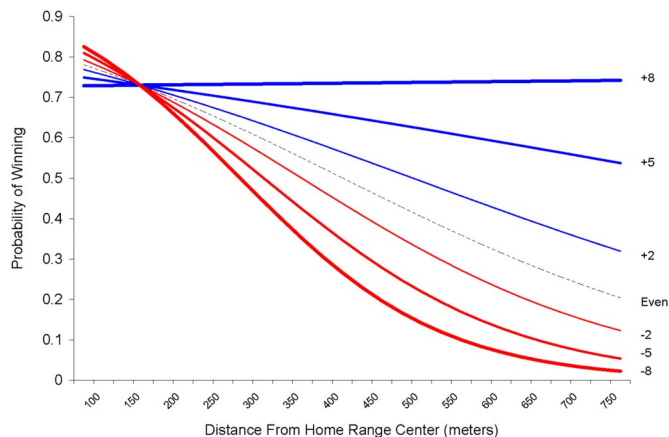


Fig. 2. Probability of winning versus distance from home range center predicted by the multiple logistic regression described in the text. Blue lines represent interactions when the focal group outnumbered its opponent, and red lines indicate when the focal group was outnumbered. The numbers and line thicknesses show the degree of asymmetry in relative group size.

interaction remained high for comparatively large groups, but decreased sharply for small groups. In other words, groups were able to overcome a numerical disadvantage and defeat relatively larger groups in central portions of their range, but were unable to do so in the periphery.

Discussion

In this study, we demonstrate that location and relative group size interact to determine the outcome of contests among social groups. Although previous research has shown that group size is an important determinant of success in intergroup competition (33–35), these studies have not investigated how RHP and payoff asymmetries interact to shape the balance of power among groups. We show that, although large relative group size increased the probability of winning intergroup interactions, the effect was not uniform across space. Differences in group size were less important in the centers of home ranges. In these areas, resident groups had a high probability of winning interactions irrespective of group size. Numerical superiority became important near home range borders where larger groups tended to prevail. These results are consistent with the predictions of individual-based models that address the role of RHP and payoff asymmetries in deciding contests. However, contests among groups are more complicated than contests between individuals because they involve the coordinated actions of multiple individuals. This additional complexity raises questions about how the observed pattern of intergroup relationships was generated.

Previous studies have shown that both participation in and intensity of capuchin intergroup contests are highly variable (19, 38, 39). In some cases, a few adult males threaten each other from the tops of trees, whereas other encounters involve many members of both sexes threatening, chasing, and grappling with one another (19, 38). Thus, variable participation based on contest location may explain why small groups are able to defeat larger groups near the center of their home range, and thus why previous studies of intergroup relationships in this species concluded that group size did not determine competitive ability (19).

We propose that intergroup contests present a collective action problem; therefore, total group size is an imperfect predictor of a group's realized RHP. The realized RHP of a group in any given contest is determined by the number of individuals who participate. Individuals, however, face a temptation to cheat and enjoy the resources gained through intergroup contests without paying the costs of competing (40–44).

This temptation should vary with the value of the resource in question. In central portions of their home range, resident groups may value contested areas more than intruders (45). Consequently, members of the resident group may have less temptation to cheat, and a larger proportion of the group may participate in intergroup contests. In contrast, because the costs of losing are hypothesized to decrease with distance from the home range center (45), members of intruding groups may experience a higher temptation to defect. In the case of a comparatively large intruding group, this tendency may have the effect of balancing the numerical odds or perhaps giving an advantage to a smaller resident group that has complete participation.

Interestingly, although geometric location within the home range affected the odds of winning, frequent use of an area did not. We assessed use in the 2-week period before an intergroup interaction. On this time scale, heavily used areas likely correspond to locations of fruiting trees (M.C.C., unpublished data). The fact that groups were neither more nor less likely to win interactions in areas they used intensely suggests that the focus of capuchin intergroup competition may be the defense of space, rather than the defense of specific food resources (38). However, unlike central place foragers or animals whose nest or den is located at the center of their home range, there is not a clear reason why the centers of capuchin home ranges would be more highly valued than peripheral regions. Home range centers may be areas of particularly high resource density, or competition with neighbors may decrease the value of resources in peripheral areas (26, 27). Additional data are needed to distinguish between these two hypotheses.

By allowing us to simultaneously track the movements of multiple capuchin social groups, the ARTS system provided the opportunity to observe a large number of intergroup encounters over a relatively short period. The large size of this dataset gave us the statistical power to test how relative group size and interaction location interact to shape intergroup relationships, a question that had previously been unanswerable because of the logistical difficulties of studying these relatively infrequent events. ARTS also provided a means to eliminate the effect of observer presence on the outcome of intergroup contests. However, because only two individuals in each study group were radio-collared, we could not use ARTS data to determine how many individuals in each group participated in each interaction. Additional observational or experimental data are needed to test the hypothesis that individuals make decisions about participating in intergroup contests on the basis of the location of the interaction and to determine whether differences in participation can explain why small groups defeat much larger groups in the center of their home ranges.

Contests between social groups influence access to resources, and thus fitness, in a wide range of group-living species, but little is known about the factors that determine how conflicts over food resources, territories, and mates are resolved. This question is particularly compelling because intergroup competition is pronounced in both human (i.e., warfare) and chimpanzee social relationships, and is therefore thought to have played a key role during human evolution (46). In human intergroup encounters, as with many social animals, numerical superiority provides a competitive advantage (2), but to our knowledge the role of interaction location (i.e., ownership) has never been explored. This study uses capuchins as a model species for understanding how relative group size and location interact to shape intergroup relationships. The tendency of resident groups to win contests may help explain how small groups are able to persist even in areas with intense intergroup competition. The dynamic interaction between the effects of relative group size and location may stabilize relationships among neighboring groups, allowing the

method identifies and excludes variation in the response variable that is due to uneven sampling of groups. For each interaction, we randomly selected one group as the focal subject for analysis.

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